

A classification system for predicting invasiveness using climatic niche traits and global distribution models: application to alien plant species in Chile

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Abstract

Functional traits that predict plant invasiveness are a central issue in invasion ecology. However, in many cases they are difficult to determine, especially for a large set of species. Climatic niche traits can overcome this problem due to the ease of acquiring them for a large number of species. This effort is critical given that knowledge of species invasiveness is necessary (although not sufficient) to anticipate/manage invasive species.

In this study, we examined thermal and hydric niche traits to predict plant invasiveness. We used a set of 49 alien plant species, representative of the alien flora of Chile. Niche traits were obtained using environmental information (WorldClim) and global occurrences. Invasiveness was estimated using global niche models and projection of the potential distribution in Chile. As a final step, we reviewed the literature for a subset of species, documenting their impacts on a) biodiversity, b) crop agriculture and c) livestock.

Thermal niche breadth and thermal niche position were the most important niche traits to predict potential distribution (a proxy of invasiveness). Using thermal niche breadth and niche position traits, we constructed a graphical model that classifies alien species as highly invasive (wide thermal niche breadth and low niche position) or low potential to be invasive (narrow niche breadth and high niche position). We also found no association between our invasiveness classification and the documented impact of alien species.

Keywords

Chile, climatic niche, alien plants, functional traits, hydric niche, invasiveness, potential distribution, thermal niche, invasion ecology

Introduction

Which traits make alien species invasive? This question has been central in invasion ecology (Drake 1989; van Kleunen et al. 2010). Amongst alien plants, morphological, functional or life history traits have often been used to explore which traits are the best predictors of invasiveness; i.e. the capacity of alien species to spread across new ranges (Rejmánek et al. 2005). However, this approach is controversial due to the difficulty of obtaining accurate and representative trait values for a large set of species (van Kleunen et al. 2010), as well as because, in some cases, their predictive value is variable, as the adaptive value of traits can be context-dependent (Daehler et al. 2004; Pyšek and Richardson 2007; van Kleunen et al. 2010).

An alternative approach has been the use of climatic niches of alien species to predict invasiveness (Castro-Díez et al. 2011; Thuiller et al. 2012). The climatic niche is defined as the set of climatic conditions within which a species is able to persist and maintain a stable population (Soberón 2007). Once an alien species arrives in a new range, climate is the first barrier it must surmount in order to establish and eventually spread across the new range (Higgins and Richardson 2014; Pearson and Dawson 2003).

According to niche-biotope duality (Colwell and Rangel 2009), species distribution models (SDMs) are appropriate tools to link niche requirements to geographic space, generating a probabilistic map that describes habitat suitability (Elith and Leathwick 2009). For alien species, these models can be used to extrapolate potential distribution from native ranges to other regions (transferability) (Peterson et al. 2011). Transferability of SDMs assumes that niches are conserved in alien species (Wiens et al. 2010); consequently, predictions should properly be made only to climate analogue regions (Di Febbraro et al. 2013; Richardson and Thuiller 2007). Moreover, the size of the area predicted by SDMs can be regarded as a *proxy* of invasiveness, as this area represents the potential area that the species might occupy (Castro-Díez et al. 2011; Lloret et al. 2004).

As alien species certainly colonise non-analogue climate regions due to niche shift (Tingley et al. 2014), it is possible to construct global species distribution models (GSDMs) using information of the totality of regions where the species have been registered (Perterra et al. 2017). Under these conditions, the niche conservatism assumption is not necessary (Gallien et al. 2012).

At a biogeographical level, two climatic niche traits can be used: (i) climatic niche breadth (i.e. the range of climate variation where a species occurs) (Gregory and Gaston 2000; Quintero and Wiens 2013) and (ii) climatic niche position (i.e. the degree of matching between climatic niche requirements and the climate in the invaded

range) (Thuiller et al. 2012). Estimating these traits requires records of species occurrences and of the climate conditions associated with such occurrences; climatic niche breadth and climatic niche position have been successfully used to predict invasiveness in other studies (Jiménez-Valverde et al. 2011; Quintero and Wiens 2013; Slatyer et al. 2013). Moreover, they can be easily estimated for a large number of species, given the huge amount of freely-accessible climate information (WorldClim: <https://www.worldclim.org/>) and the availability of occurrence data for invasive species worldwide (GISD; <http://www.iucngisd.org/gisd/search.php>).

Chile is currently home to a large and rapidly increasing number of alien plants; more than 700 alien vascular plants have been recorded (Fuentes 2014; Fuentes et al. 2013). Additionally, Chile contains a notable variation in climate regions (Di Castri and Hajek 1976), so it constitutes an ideal scenario for invasion by alien plants from different biogeographic regions of the world (Fuentes 2014). In particular, Chile has a wide range of temperatures and precipitation along elevation and latitude gradients, so climatic niche traits ought to be critical for an understanding of the invasive potential of alien plants in Chile (Cuesta et al. 2019).

The term invasiveness is often correlated positively with harmful impacts on biodiversity, economy or health. This may be because, as a species spreads across a larger area, it has a greater probability of producing detrimental effects on the environment (Ortega and Pearson 2005; Ricciardi et al. 1996); however, the evidence indicates that, in some cases, this is not the situation (Ricciardi and Cohen 2007). Therefore, the assumption that invasiveness implies harmful impact needs to be tested case by case.

Making a distinction between invasiveness and impact is critical for management. The Chilean government has identified various different actions needed for the management of invasive species in Chile. One of them is to conduct basic and applied research to develop validated procedures to study invasiveness and risk analysis for hundreds of alien species living in aquatic and terrestrial ecosystems (“Estrategia Nacional de Biodiversidad” (2017–2030). The information about GSDMs of alien species and methods we have proposed in this study should contribute to these needs by calculating the “likelihood” of aliens to spread, as well as the climatic determinants of such spread (Benito et al. 2009; Settele et al. 2005).

In this study, we have examined climatic niche traits to predict invasiveness for a set of alien plants in Chile. In order to do so, we used global climate information to obtain the thermal and hydric niche breadth and position of 49 species and GSDMs to predict the sizes of their distribution areas in Chile. We summarise this information in a predictive framework that enables us to classify species as having either high or low predicted invasiveness. In addition, we have explored the association between invasiveness and impact using our results and impact information obtained from literature.

Methods

The stages followed to collect and analyse data are summarised in Fig. 1.

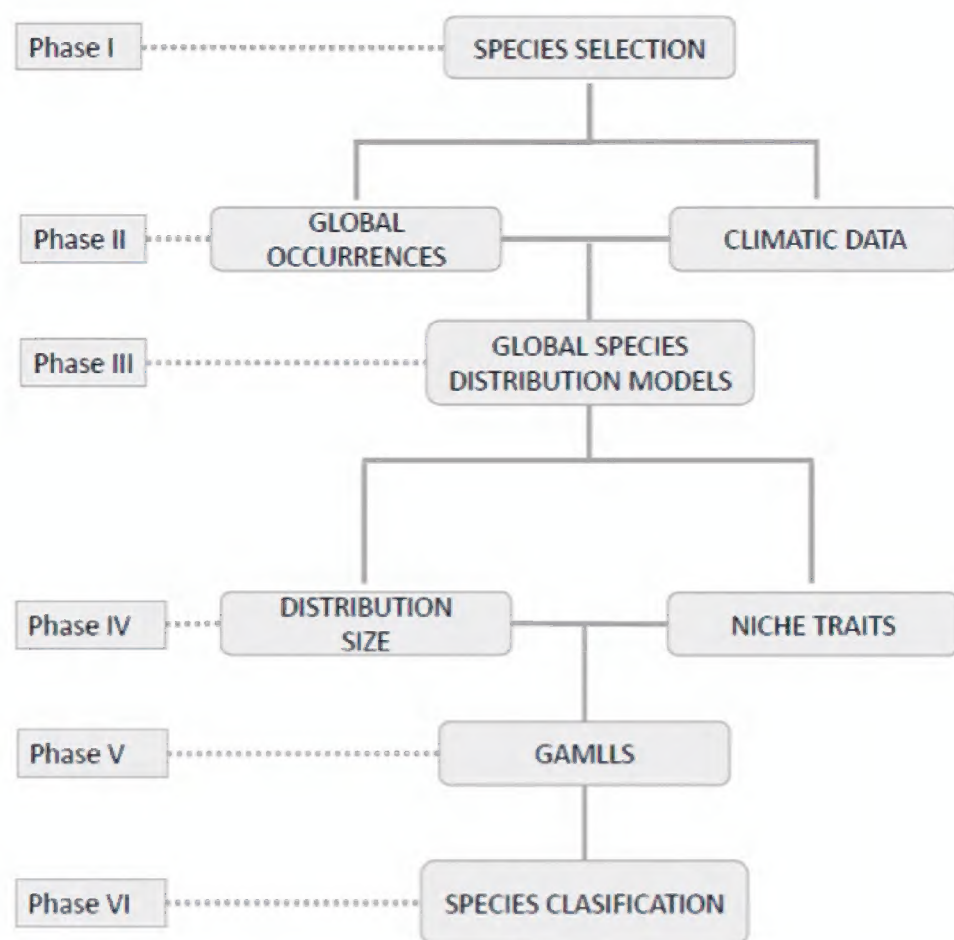


Figure 1. Flow chart which represent the different methodological phases followed in this study.

Phase I (Species selection)

The number of alien species selected for this study was 49; two shrubs and 47 herbs (see Suppl. material 2 for the scientific names). We focused mainly on herbs because they constitute 90.4% of alien plants in Chile (53.4% annuals and 42% perennials) and because there is considerable knowledge about their ecology and distribution (Matthei et al. 1995). We did not include more woody plants because there is little information on their invasive status or their biogeography (Fuentes 2014; Fuentes et al. 2013; Matthei et al. 1995; Quiroz et al. 2009). The 49 alien plant species used in this study belong to 19 families, with Poaceae (10 spp), Asteraceae (8 spp), Fabaceae (5 spp) and Caryophyllaceae (4 spp) the most numerous, constituting 55% of the total species.

Phase 2 (Global occurrences and climate data)

The 49 alien species were obtained from published information (Castro et al. 2005; Fuentes et al. 2013); these species were selected *a priori* to include species with narrow, medium and broad recorded distributions in Chile (see Suppl. material 1). We collected occurrence data for each species from the Global Biodiversity Information Facility (<http://www.gbif.org/>) and 'Sp. Link' (<http://splink.cria.org.br/>) to obtain species occurrences at the global scale. For Chile (regional scale), occurrence data were recorded from herbaria located at the University of Concepción and the National Museum of Natural History, Santiago de Chile. For both global and regional scales, we

ensured the validity of the occurrence data by eliminating duplicates and discarding points that were located in the ocean, snow or rock. We reduced the spatial dependence of data, creating a buffer zone (0.09 degrees) around each occurrence point, thus leaving points at least 10 km apart. Despite the reduction of occurrence points, we kept a reasonable amount of data for SDM analysis (from 208 occurrences for *Datura ferox* to 6429 for *Cirsium vulgare*). For the construction of global models, we used the totality of occurrences.

The climate information required for the GSDMs was obtained from WorldClim (Hijmans et al. 2005). There are 19 variables available in WorldClim; however, to avoid change by model over-fitting, we used a Spearman correlation test (Holt et al. 2009) restricting the climate parameters to pairs of variables with correlation values ≤ 0.7 . In these cases, we selected the climate variable with the higher biological relevance (Merow et al. 2013). The selected variables were maximum temperature of the warmest month (BIO5), minimum temperature of the coldest month (BIO6), mean maximum temperature of the warmest month (BIO7), mean annual precipitation (BIO12), precipitation of the driest month (BIO14) and precipitation in the warmest quarter (BIO18).

Phase III (Global species distribution models)

From the *GSDMs*, we estimated alien plant invasiveness using the size of the potential distribution area as a *proxy*. We used MaxEnt software, which implements a machine-learning method that enables potential distribution to be predicted using only presences, under the principle of maximal entropy (Phillips et al. 2006). GSDMs are used to examine species niche potentials, detecting new environments where species occur in invaded regions, but they do not occur in native ranges due to dispersal limitation, biotic interactions or simply because they no longer exist in the native range (Gallien et al. 2012).

The climate envelope of the GSDMs included the climates of the five continents (excluding Antarctica), so for each model, we increased the number of pseudo-absences to 10,000, following Merow et al. (2013) and reduced the magnitude of the regulator to 0.5 (Merow et al. 2013; Phillips and Dudík 2008). To quantify the potential distribution size (in km²), we selected the average model obtained from 25 bootstrap replicates; for each replicate, we used 70% of the occurrences for training and 30% for testing the model (Phillips et al. 2006; Thuiller et al. 2005). To validate the capacity of average models to discriminate between false positives and false negatives, we used the criteria of Thuiller et al. (2005) for AUC values, being the most common test for SDMs. If AUC = 0.5, then the model does not have discrimination capacity (Phillips and Dudík 2008). When AUC is between 0.5 and 0.7, the model has poor discrimination capacity; if AUC values are between 0.7 and 0.9, then the model has a reasonable discrimination capacity; values higher than 0.9 indicate a model with a very good discrimination ability (Pierce and Ferrier 2000). In addition, we calculated the Boyce Index for each average model. This Index is a threshold-independent accuracy estimator which uses the Spearman rank coefficient to correlate the occurrence points vs. the predicted areas for two datasets (Boyce et al. 2002). If the Index is posi-

tive for a model, then its predictions are consistent with the distribution of presences in the evaluation dataset. If the values are close to zero, then the model is no different from a random model; when values are negative, then there are counter-predictions (Hirzel et al. 2006).

Binary projections to discern suitable/unsuitable habitats that are generated by different thresholds in SDMs may differ drastically; therefore, choosing the correct threshold is not arbitrary (Liu et al. 2005; Magory Cohen et al. 2019). For instance, in some studies, the thresholds are selected by simulations (Liu et al. 2005), others use several thresholds simultaneously (Escalante et al. 2013), while others consider the importance of omission/commission errors (Norris 2014). Given that we aimed to model the alien species' full potential to invade in Chile, we selected the threshold that minimises the omission error; i.e. the minimum training presence provided by Max-Ent (0% omission rate); this threshold has been used successfully in other studies using GSDMs (Magory Cohen et al. 2019).

Phase IV (Distribution size and niche traits)

From climate information obtained from WorldClim (Hijmans et al. 2005) and species occurrences obtained from data bases, we calculated climatic niche breadth and position for the alien species, looking for the occurrences with the maximal and minimal observable climate values (Quintero and Wiens 2013). Thermal niche breadth (*TNB*) was estimated for each species by subtracting the maximum temperature in the warmest month (*BIO5*) from the minimum temperature of the coldest month (*BIO6*).

$$\text{TNB Species } i = (\max \text{BIO5} - \min \text{BIO6}) \quad (1)$$

Hydric niche breadth (*HNB*) was estimated by subtracting the maximum precipitation in the wettest month (*BIO13*) from the minimum precipitation in the driest month (*BIO14*)

$$\text{HNB Species } i = (\max \text{BIO13} - \min \text{BIO14}) \quad (2)$$

We defined the thermal niche position of species *i* (*TNP_i*) as the difference (or distance) between the mean thermal niche and the mean annual temperatures in Chile (Eq. 3). Similarly, the hydric niche position (*HNP_i*) is the difference (or distance) between the mean hydric niche and the mean annual precipitation in Chile (Eq. 4). (Phase 4, Fig. 1).

$$\text{TNP}_i \text{ Species } i = \left(\frac{\max \text{BIO5} + \min \text{BIO6}}{2} \right) - \text{Chile} \left(\frac{\max \text{BIO5} + \min \text{BIO6}}{2} \right) \quad (3)$$

$$\text{HNP}_i \text{ Species } i = (\max \text{BIO13} + \min \text{BIO14}) / 2 - \text{Chile} (\max \text{BIO13} + \min \text{BIO14} / 2) \quad (4)$$

Phase V (GAMLSS)

We related potential distribution size to thermal and hydric niche traits. The distribution size data followed a Weibull distribution (see Suppl. material 1: Table S1 and Suppl. material 3: Fig. S1). We fitted a general additive model for location, scale and shape (GAMLSS) (Rigby and Stasinopoulos 2005) using the GAMLSS package in R, which supports the Weibull distribution (Stasinopoulos and Rigby 2007).

Phase VI (Species classification)

We summarised our results in a bi-dimensional plane including species position in relation to the two most important climatic niche traits. Our aim was to provide a predictive tool to classify species invasiveness using only climatic niche traits. We are aware that there are factors other than climate that may determine invasion success; however, climate is the first barrier for colonisation. Following validation, this approach could provide a rapid screen to measure invasiveness for a large number of alien species (animals and plants) in a short time. We standardised the niche traits for species using the algorithm:

$$\frac{(NT_i - aNT)}{\sigma NT},$$

where NT_i represents niche traits of species i (thermal or hydric niche amplitude or position); aNT is the average niche trait estimated for the 49 species and σNT is the standard error of NT . In this way, the plane is divided into four regions. In Quadrant I, TNB values are negative and TNP values are positive; species that fall into this zone have low invasive potential. In Quadrant IV, TNB values are positive and TNP values are negative; species that fall into this zone have high invasive potential. Quadrant II and Quadrant III contain the species with intermediate invasive potentiality (for more details see the text in Fig. 4).

To determine whether there is an association between predicted invasiveness, based on climatic niche and impacts of alien species, we conducted literature reviews to assess evidence of impact during the last 30 years. The impact was measured qualitatively; that is, whether there was any documentation of impacts or not. We classified impact into three general categories: (i) on biodiversity, (ii) on crop agriculture and (iii) on livestock.

We searched for evidence of impact of alien species that fall within Quadrant I (low invasiveness) and Quadrant IV (high invasiveness) (Fig. 4). We used a X^2 test (1 d.f.) for proportions to compare the probability of impact between species with low invasiveness vs. species with high invasiveness. For this analysis, we pooled the information for the three different kinds of impact. To collect impact information, we searched Google Scholar using the terms *Scientific name AND Invasive AND Impact*.

Results

GSDMs

The performance of the GSDMs was quite good as measured by the AUC values (average = 0.977; SD = 0.014) and the Boyce Index (average = 0.970; SD = 0.06) (for detailed data, see Suppl. material 1). The potential distribution sizes in Chile ranged from 763,778 km² for *Spergula arvensis* (Caryophyllaceae) to 43,473 km² for *Atriplex nummularia* (Amaranthaceae) (Fig. 2A, C). The average size was 568,420 km². In 31 species (63% of the total), the distribution size for the species was higher than average; the families that contributed most to this sub-group were Poaceae, (7 spp), Asteraceae (5 spp), Fabaceae (3 spp) and Caryophyllaceae (3 spp) (for some examples, see Fig. 2C, D). The distribution sizes of 18 species were lower than the average (37% of the total) and the most numerous families for these species were Asteraceae (3 spp), Poaceae (3spp), Amaranthaceae (3 spp) and Fabaceae (2 spp).

GAMLSS

We detected significant positive effects of *TNB* on potential distribution size (Table 1, Fig. 3A), but no significant effects were detected for hydric niche breadth or position (Table 1; Fig. 3C , D). The effects of *TNP* on potential distribution size were negative, but not statistically significant (Table 1). As the p-value for this trait was close to $\alpha = 0.05$ ($p = 0.08$), we decided to correlate *TNP* with the potential distribution size independently; we detected a significant negative correlation (Pearson’s product-moment = -0.62; $t = -5.4527$, d.f. = 47, $p < 0.001$; Fig. 3B).

Species classification

Standardised *TNP* and standardised *TNB* were negatively correlated (Pearson; $r = -0.69$, $p < 0.001$; Fig. 4). In Quadrant I; i.e. the zone of low invasiveness, there are 19 species (38% of the total species); the most-represented families are Fabaceae (2 spp), Poaceae (3 spp) and Asteraceae (3 spp). Distribution size for 82% of these 19 species was lower than the average (grey spots in Quadrant I, Fig. 4). In Quadrant IV, the sector that corresponds to the highest predicted level of invasiveness, there are 20 species (41% of the

Table 1. GAMLSS for testing the effect of thermal and hydric niche traits on potential distribution predicted from global niche models on 49 alien plant species in Chile. The pseudo-R² of the model was 0.45.

Factors	Estimate	Standard error	t – value	p – value
Intercept	12.659	0.640	19.786	<< 0.001
Thermal niche breadth (TNB)	0.022	0.009	2.526	0.016
Thermal niche position (TNP)	-0.043	0.024	-1.798	0.082
Hydric niche breadth (HNB)	-0.0006	0.0008	-0.798	0.429
Hydric niche position (HNP)	-0.001	0.002	-0.470	0.641

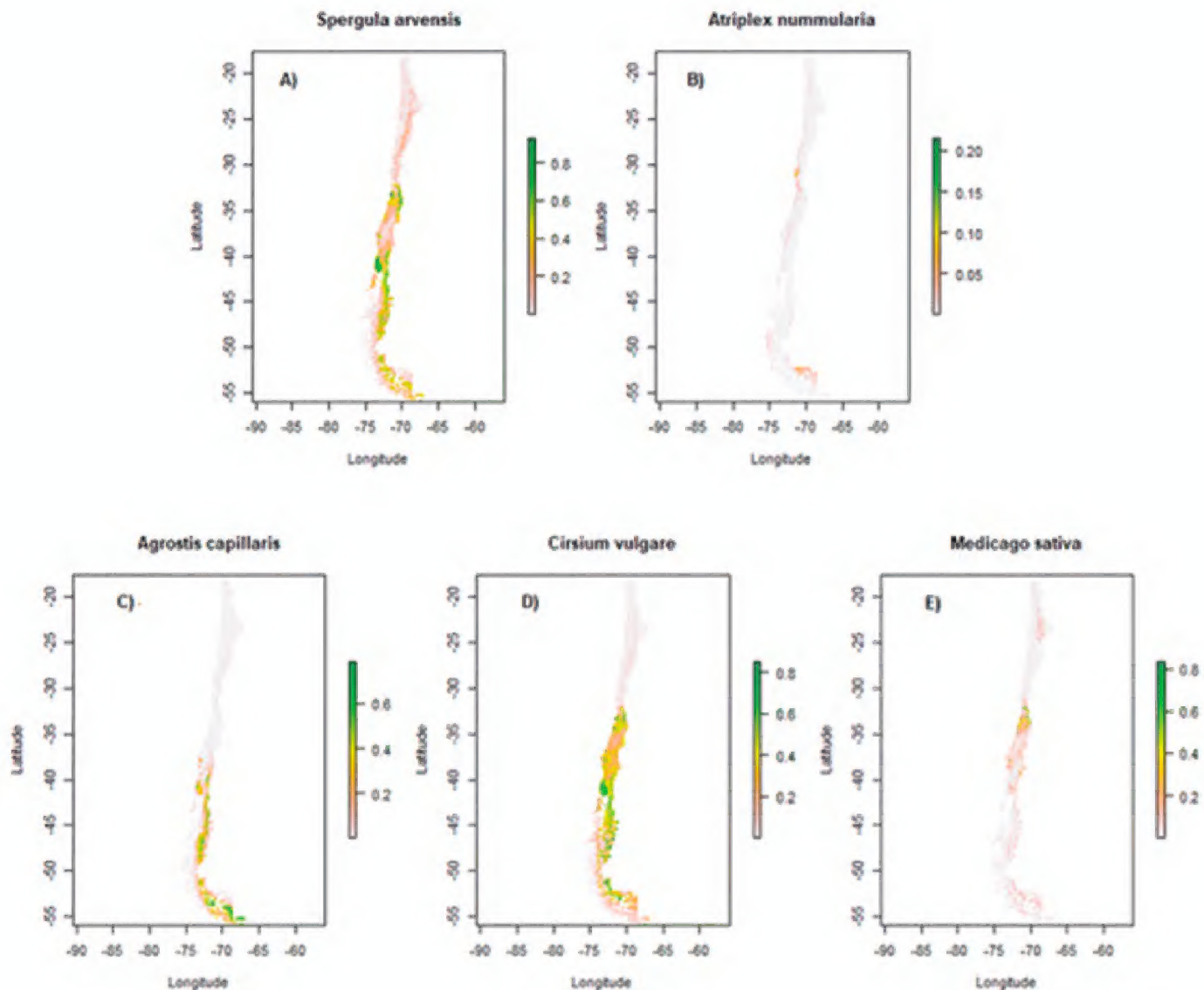


Figure 2. Global Species Distribution Models (GSDMs) projected in Chile for a sub-set of species **A** *Spargula arvensis* (the highest distribution size) **B** *Atriplex nummularia* (the lowest distribution size) **C** *Agrostis capillaris* (representative of Poaceae) **D** *Cirsium vulgare* (representative of Asteraceae) **E** *Medicago sativa* (representative of Fabaceae). For the rest of exotic species, see Suppl. material 2.

species); the most-represented families are Fabaceae (3 spp), Poaceae (5 spp) and Asteraceae (3 spp). The predicted distribution size for all of these species was higher than the average (black spots in Fig. 4). The rest of the 10 species were located in Quadrants II and III; i.e. intermediate level of invasiveness. For a summary of alien plants located in Quadrant 1 and 4, see Table 2.

Invasiveness and impact

We detected no association between predicted Invasiveness (based on quadrant position, Figure 4) and impact (obtained from literature) of alien species ($X^2 = 0.02$, d.f. = 1 $p = 0.85$; Table 3). In fact, of the total number of species documented to have some impact in Chile ($n = 23$; see Table 3), 58% ($n = 11$) of them were classified as having low invasiveness or being non-invasive and 60% ($n = 12$) were classified as having high invasiveness; these percentage values were not statistically significant (Z score = -0.34 , $p = 0.90$). (For the details of species, impacts and references, see Suppl. material 2).

Table 2. List of alien plant species which fall into Quadrant I (low invasiveness) and Quadrant IV (highly invasiveness), according to the classification obtained from Figure 4.

Species with low invasiveness (Quadrant I)	Species with high invasiveness (Quadrant IV)
<i>Ammi visnaga</i>	<i>Aira caryophylllea</i>
<i>Atriplex nummularia</i>	<i>Bromus catharticus</i>
<i>Atriplex suberecta</i>	<i>Bromus sterilis</i>
<i>Carthamus lanatus</i>	<i>Cardamine hirsuta</i>
<i>Conyza bonariensis</i>	<i>Cirsium vulgare</i>
<i>Cynosurus echinatus</i>	<i>Convolvulus arvensis</i>
<i>Datura ferox</i>	<i>Daucus carota</i>
<i>Dolichos lignosus</i>	<i>Erodium cicutarium</i>
<i>Fumaria agraria</i>	<i>Galium aparine</i>
<i>Lupinus arboreus</i>	<i>Hordeum jubatum</i>
<i>Mesembryanthemum crystallinum</i>	<i>Matricaria discoidea</i>
<i>Pennisetum clandestinum</i>	<i>Medicago sativa</i>
<i>Ruta chalepensis</i>	<i>Polypogon monspeliensis</i>
<i>Sanguisorba minor</i>	<i>Rumex longifolius</i>
<i>Scirpus mucronatus</i>	<i>Sonchus asper</i>
<i>Sonchus tenerrimus</i>	<i>Spergula arvensis</i>
<i>Spergularia media</i>	<i>Stellaria media</i>
<i>Stellaria pallida</i>	<i>Veronica scutellata</i>
<i>Vulpia muralis</i>	<i>Vicia sativa</i>
	<i>Vicia villosa</i>

Table 3. Contingency table showing the number of alien species cross-classified by invasiveness and impact: a) low invasiveness and high invasiveness: the counts were obtained from Quadrant 1 and Quadrant 4; Figure 4; b) species recorded with some impact and species with no impact (for the list of species and the references, see Suppl. material 2).

	Impact	No impact	Total
Low invasiveness	11	8	19
High invasiveness	12	8	20
Total	23	16	39

Discussion

In our study, we examined the importance of thermal and hydric niche traits to predict alien plant invasiveness. We have also provided a simple protocol for a rapid assessment of invasiveness. We will discuss our results in light of plant physiology, the use of SDMs in terms of advantages and limitations of our study to support the control and management of alien species.

One surprising result was that hydric niche traits were not important for explaining predicted plant distribution area (Schulze et al. 1987; Turnbull et al. 2000). Most of the species we examined have a herbaceous life form (with the exception of two *Atriplex* species); these plants have regeneration tissues that are more sensitive to thermal stress than to water limitations, contrary to expectations for woody plant species (Turnbull et al. 2000). In particular, reproductive phenology – specifically flower development, pollen release and germination and seed and fruit maturation in herbaceous plants – are particularly sensitive to temperature variation (Körner et al. 2016). Despite the important influence of temperature on plant performance, there are only

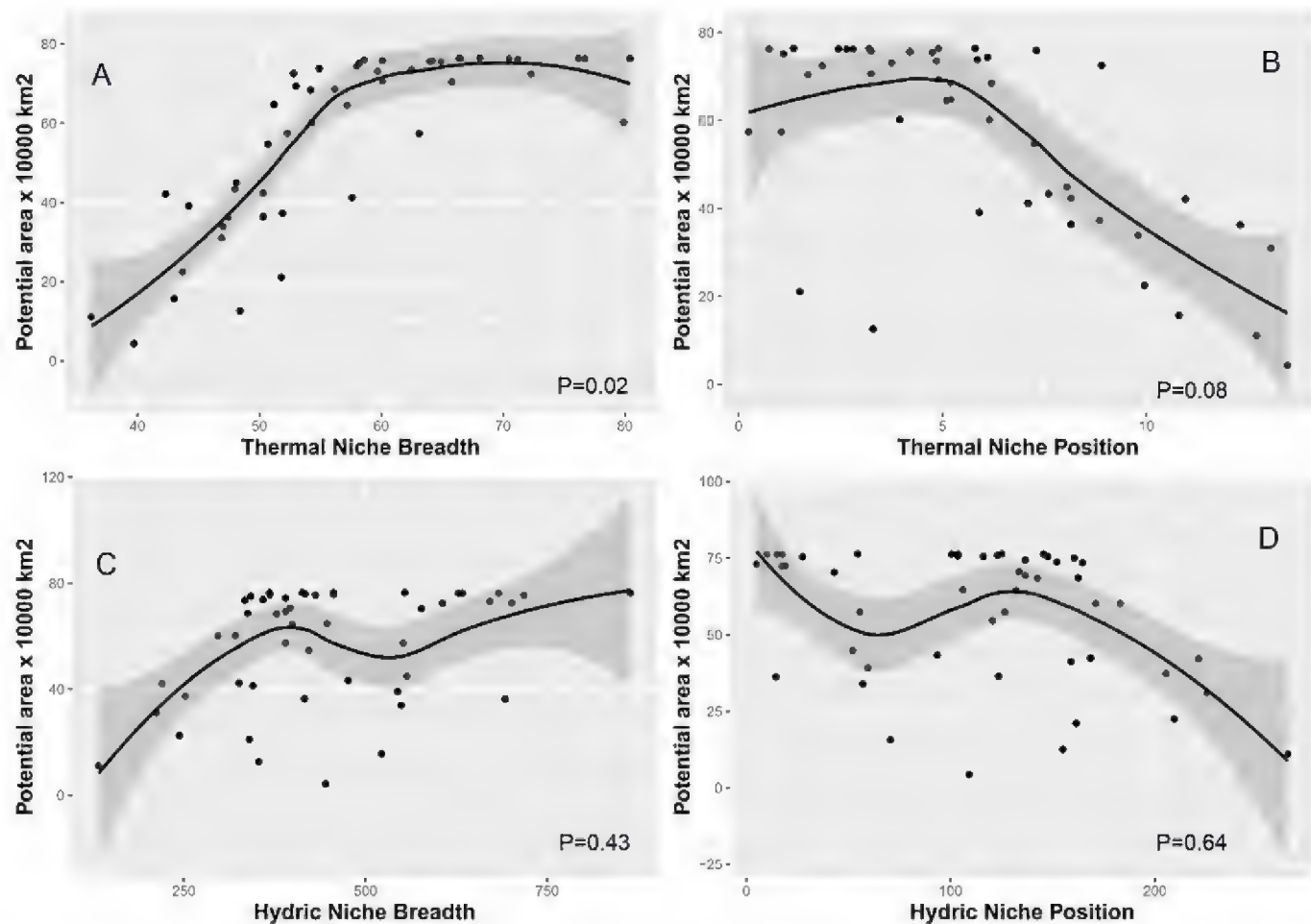


Figure 3. Relation of niche traits and Potential distribution size ($\times 10000$) in km^2 , for a set of 49 exotic plants occurring in Chile **A** Thermal niche breadth **B** Thermal niche position **C** Hydric niche breadth **D** Hydric niche position. We detected significant effects for Thermal niche breadth and position. The p-values were obtained from GAMLSS. Confident intervals were constructed with LOESS regression analysis.

a few studies that have scaled the effect of temperature on the biogeography of plants (Bykova et al. 2012; Pigott 1989; Rasmussen and Kollmann 2004).

Climatic niche breadth has frequently been used to predict invasiveness (“niche breadth-invasion success hypothesis”) (Granot et al. 2017; Vazquez 2006). Similar results have also been obtained for native plants, where climatic niche traits are good predictors of the biogeographic expansion of native trees (Vela Díaz et al. 2020). Our results showed that this is the case for alien species in Chile. Specifically, using thermal niche traits (breadth and position), we propose a suitable classification scheme to categorise the invasive status of alien plants in Chile: a) species in Quadrant IV (Fig. 4) are the best candidates to be highly invasive and b) species in Quadrant I (Fig. 4) will probably be less invasive.

Determining which traits promote plant invasiveness is a central issue in biological invasion research (Daehler 2001; Duncan et al. 2001; Rejmánek et al. 2005). However, evaluating these factors implies a lengthy effort that does not match the timetable required for management practices, especially if anticipation is the most fundamental strategy to control species invasions (Leung et al. 2005). In our study, we found that thermal niche traits can be used for a rapid assessment of the invasive status of alien species in Chile, thereby helping to provide information for management practices.

Incorporating global climate data into GSDMs is essential for a reasonable approximation of a species’ potential to invade across different regions beyond its native

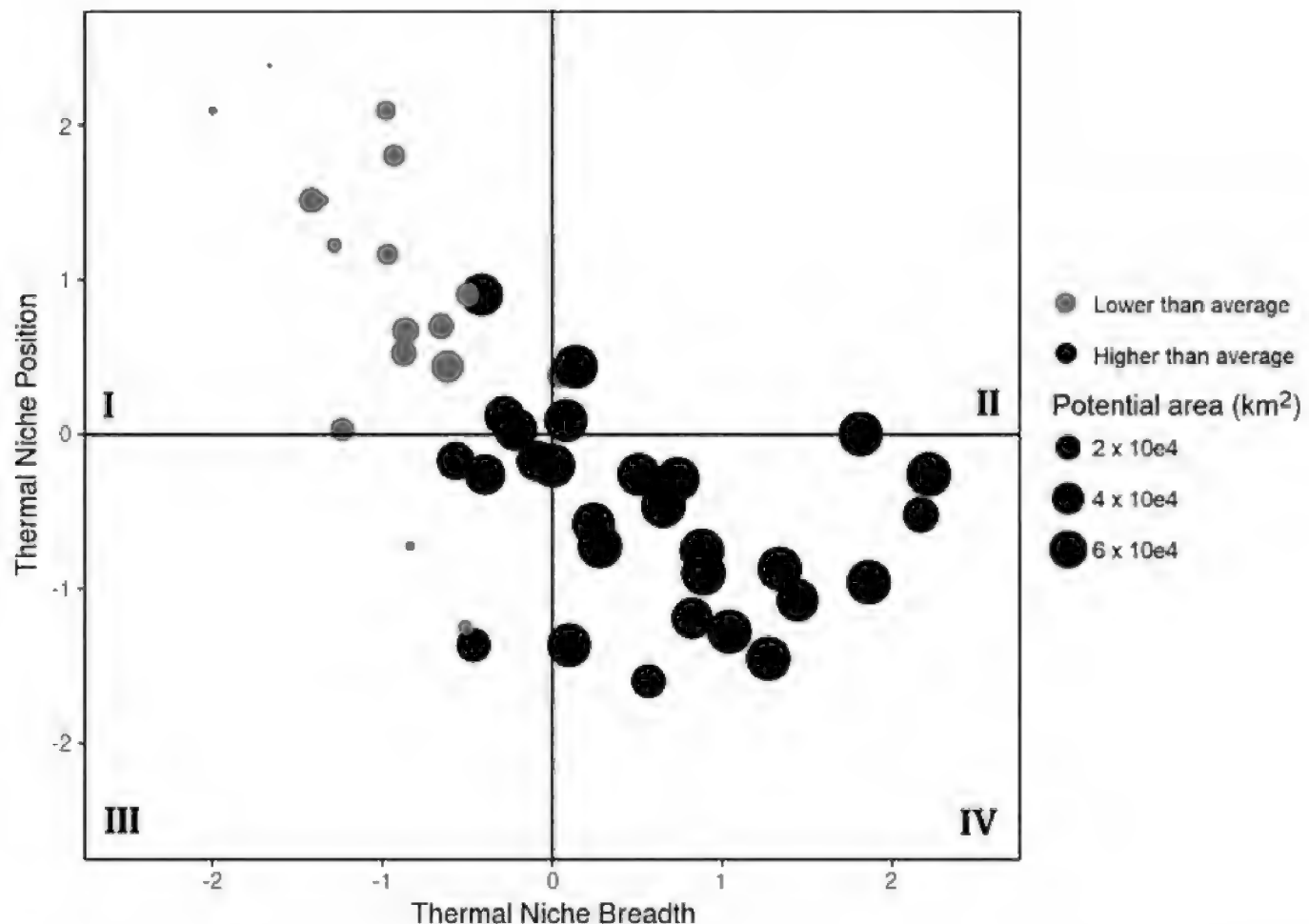


Figure 4. Summary of species position in a bidimensional-plane whose axes are standardized thermal niche breadth and thermal niche position from a sample of 49 exotic plants in Chile. Niche values were standardized using the expression $((NT)_{-1} - aNT) / \sigma NT$. The point (0, 0) represents the average values of both niche traits. Quadrant I represent the area of low invasiveness; Quadrant IV represents the area of high invasiveness. Dots represent the position of species within the two-phase plane. Dots size represents species distribution size. Gray dots: species with distribution size lower than average; black dots: species with distribution size higher than average.

ranges (Kambach et al. 2019; Lombaert et al. 2011). GSDMs can help us to understand the big picture of biogeographic patterns; however, they are unable to show the role of local processes in the details of species distribution, such as topography (elevation and slope exposure (Önol 2012)); anthropogenic disturbances such as deforestation, fires and fragmentation (Franklin 2010); and biotic interactions and dispersal limitation (Boulangeat et al. 2012).

Caveats

Invasiveness assessment is an important input for alien species management; however, for a more comprehensive approach, we need to know impacts. For most people (i.e. stakeholders and policy-makers), invasiveness and impact are synonymous (Colautti et al. 2004; Ricciardi and Cohen 2007), despite weak evidence for a connection between these two concepts (Ricciardi and Cohen 2007; Williamson and Fitter 1996). In our study, we did not find a significant association between invasiveness and impact (Table 3), although we are aware that our analysis is preliminary and requires further

examination of a larger number of species. However, for application purposes, we can propose target species for management to prevent detrimental effects on crop agriculture, livestock or biodiversity, based on our literature review (Table 2).

We propose to focus primarily on the 12 species that were predicted to be highly invasive and, at the same time, were documented to have impacts (see Table 2): *Airacaryophyllea*, *Bromus catharticus*, *Cirsium vulgare*, *Erodium cicutarium*, (outcompete native plants); *Convolvulus arvensis*, *Sonchus asper* (crop weed or pest); *Medicago sativa*, *Polipogon monspeliensis*, *Spergula arvensis*, *Stellaria media* (allelopathic effects) and *Hordeum jubatum*, *Sonchus asper* and *Vicia villosa* (poisonous to livestock) (for details and references, see Suppl. material 2).

The issue of the impact of invasive plant species is the subject of an ongoing interdisciplinary research programme (Settele et al. 2005); however, the basic questions remain open up to date ; namely, what are the impacts of invasion and are there some traits that can be used to anticipate impacts? The search for species attributes seems to be an interesting avenue. For instance, in plants, life form, stature and pollination syndrome together with the network structure formed between plants and pollinators are regarded as useful predictors of impacts (Gibson et al. 2012; Hejda et al. 2017; Pyšek et al. 2012; Valdovinos et al. 2018).

Conclusions

In our study, we have demonstrated the importance of thermal niche traits for predicting alien plant invasiveness. Based on these results, we have proposed a conceptual framework that classifies species according to their anticipated level of invasiveness. For management purposes and to assess comprehensive risk, it is mandatory to also implement impact assessment because higher invasiveness does not necessarily imply higher impact.

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References

- Benito BM, Martínez-Ortega MM, Muñoz LM, Lorite J, Peñas J (2009) Assessing extinction-risk of endangered plants using species distribution models: a case study of habitat depletion caused by the spread of greenhouses. *Biodiversity and Conservation* 18: 2509–2520. <https://doi.org/10.1007/s10531-009-9604-8>

- Boulangeat I, Gravel D, Thuiller W (2012) Accounting for dispersal and biotic interactions to disentangle the drivers of species distributions and their abundances: The role of dispersal and biotic interactions in explaining species distributions and abundances. *Ecology Letters* 15: 584–593. <https://doi.org/10.1111/j.1461-0248.2012.01772.x>
- Boyce MS, Vernier PR, Nielsen SE, Schmiegelow FKA (2002) Evaluating resource selection functions. *Ecological Modelling* 157: 281–300. [https://doi.org/10.1016/S0304-3800\(02\)00200-4](https://doi.org/10.1016/S0304-3800(02)00200-4)
- Bykova O, Chuine I, Morin X, Higgins SI (2012) Temperature dependence of the reproduction niche and its relevance for plant species distributions. *Journal of Biogeography* 39: 2191–2200. <https://doi.org/10.1111/j.1365-2699.2012.02764.x>
- Castro-Díez P, Langendoen T, Poorter L, Saldaña-López A (2011) Predicting Acacia invasive success in South Africa on the basis of functional traits, native climatic niche and human use. *Biodiversity and Conservation* 20: 2729–2743. <https://doi.org/10.1007/s10531-011-0101-5>
- Castro SA, Figueroa JA, Muñoz-Schick M, Jaksic FM (2005) Minimum residence time, biogeographical origin, and life cycle as determinants of the geographical extent of naturalized plants in continental Chile. *Diversity and Distributions* 11: 183–191. <https://doi.org/10.1111/j.1366-9516.2005.00145.x>
- Colautti RI, Ricciardi A, Grigorovich IA, MacIsaac HJ (2004) Is invasion success explained by the enemy release hypothesis? *Ecology Letters* 7: 721–733. <https://doi.org/10.1111/j.1461-0248.2004.00616.x>
- Colwell RK, Rangel TF (2009) Colloquium Papers: Hutchinson's duality: The once and future niche. *Proceedings of the National Academy of Sciences* 106: 19651–19658. <https://doi.org/10.1073/pnas.0901650106>
- Cuesta F, Tovar C, Llambí LD, Gosling WD, Halloy S, Carilla J, Muriel P, Meneses RI, Beck S, Ulloa Ulloa C, Yager K, Aguirre N, Viñas P, Jácome J, Suárez-Duque D, Buytaert W, Pauli H (2019) Thermal niche traits of high alpine plant species and communities across the tropical Andes and their vulnerability to global warming. *Journal of Biogeography*: jbi.13759. <https://doi.org/10.1111/jbi.13759>
- Daehler CC (2001) Two ways to be an invader, but one is more suitable for ecology. *Bulletin of the Ecological Society of America* 82: 101–102
- Daehler CC, Denslow JS, Ansari S, Kuo H-C (2004) A risk-assessment system for screening out invasive pest plants from Hawaii and other Pacific Islands. *Conservation Biology* 18: 360–368. <https://doi.org/10.1111/j.1523-1739.2004.00066.x>
- Di Castri F, Hajek ER (1976) Bioclimatología de Chile. Vicerrectoría Académica de la Universidad Católica de Chile Santiago, Chile.
- Di Febbraro M, Lurz PWW, Genovesi P, Maiorano L, Girardello M, Bertolino S (2013) The use of climatic niches in screening procedures for introduced species to evaluate risk of spread: A case with the American Eastern Grey Squirrel. *PLoS ONE* 8: e66559. <https://doi.org/10.1371/journal.pone.0066559>
- Drake JA (1989) Biological invasions: a global perspective. Published on behalf of the Scientific Committee on Problems of the Environment (SCOPE) of the International Council of Scientific Unions (ICSU) by Wiley, Chichester ; New York, 525 pp.

- Duncan RP, Bomford M, Forsyth DM, Conibear L (2001) High predictability in introduction outcomes and the geographical range size of introduced Australian birds: a role for climate. *Journal of Animal Ecology* 70: 621–632. <https://doi.org/10.1046/j.1365-2656.2001.00517.x>
- Elith J, Leathwick JR (2009) Species Distribution Models: Ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics* 40: 677–697. <https://doi.org/10.1146/annurev.ecolsys.110308.120159>
- Escalante T, Rodríguez-Tapia G, Linaje M, Illoldi-Rangel P, González-López R (2013) Identification of areas of endemism from species distribution models: threshold selection and Nearctic mammals. *TIP Revista Especializada en Ciencias Químico-Biológicas* 16: 5–17. [https://doi.org/10.1016/S1405-888X\(13\)72073-4](https://doi.org/10.1016/S1405-888X(13)72073-4)
- Estrategia Nacional de Biodiversidad (2017–2030) Ministerio del Medio Ambiente, Chile, 98 pp.
- Franklin J (2010) Moving beyond static species distribution models in support of conservation biogeography: Moving beyond static species distribution models. *Diversity and Distributions* 16: 321–330. <https://doi.org/10.1111/j.1472-4642.2010.00641.x>
- Fuentes N (2014) Plantas invasoras del centro-sur de Chile: Una guía de campo. Laboratorio de Invasiones Biológicas.
- Fuentes N, Pauchard A, Sánchez P, Esquivel J, Marticorena A (2013) A new comprehensive database of alien plant species in Chile based on herbarium records. *Biological Invasions* 15: 847–858. <https://doi.org/10.1007/s10530-012-0334-6>
- Gallien L, Douzet R, Pratte S, Zimmermann NE, Thuiller W (2012) Invasive species distribution models – how violating the equilibrium assumption can create new insights: Beyond the equilibrium assumption of SDMs. *Global Ecology and Biogeography* 21: 1126–1136. <https://doi.org/10.1111/j.1466-8238.2012.00768.x>
- Gibson MR, Richardson DM, Pauw A (2012) Can floral traits predict an invasive plant's impact on native plant-pollinator communities? *Journal of Ecology* 100: 1216–1223. <https://doi.org/10.1111/j.1365-2745.2012.02004.x>
- Granot I, Shenkar N, Belmaker J (2017) Habitat niche breadth predicts invasiveness in solitary ascidians. *Ecology and Evolution* 7: 7838–7847. <https://doi.org/10.1002/ece3.3351>
- Gregory RD, Gaston KJ (2000) Explanations of commonness and rarity in British breeding birds: separating resource use and resource availability. *Oikos* 88: 515–526. <https://doi.org/10.1034/j.1600-0706.2000.880307.x>
- Hejda M, Hanzelka J, Kadlec T, Štrobl M, Pyšek P, Reif J (2017) Impacts of an invasive tree across trophic levels: Species richness, community composition and resident species' traits. *Diversity and Distributions* 23: 997–1007. <https://doi.org/10.1111/ddi.12596>
- Higgins SI, Richardson DM (2014) Invasive plants have broader physiological niches. *Proceedings of the National Academy of Sciences* 111: 10610–10614. <https://doi.org/10.1073/pnas.1406075111>
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25: 1965–1978. <https://doi.org/10.1002/joc.1276>
- Hirzel AH, Le Lay G, Helfer V, Randin C, Guisan A (2006) Evaluating the ability of habitat suitability models to predict species presences. *Ecological Modelling* 199: 142–152. <https://doi.org/10.1016/j.ecolmodel.2006.05.017>

- Holt AC, Salkeld DJ, Fritz CL, Tucker JR, Gong P (2009) Spatial analysis of plague in California: niche modeling predictions of the current distribution and potential response to climate change. *International Journal of Health Geographics* 8: 38. <https://doi.org/10.1186/1476-072X-8-38>
- Jiménez-Valverde A, Peterson AT, Soberón J, Overton JM, Aragón P, Lobo JM (2011) Use of niche models in invasive species risk assessments. *Biological Invasions* 13: 2785–2797. <https://doi.org/10.1007/s10530-011-9963-4>
- Kambach S, Lenoir J, Decocq G, Welk E, Seidler G, Dullinger S, Gégout J-C, Guisan A, Pauli H, Svenning J-C, Vittoz P, Wohlgemuth T, Zimmermann NE, Bruehlheide H (2019) Of niches and distributions: range size increases with niche breadth both globally and regionally but regional estimates poorly relate to global estimates. *Ecography* 42: 467–477. <https://doi.org/10.1111/ecog.03495>
- Körner C, Basler D, Hoch G, Kollas C, Lenz A, Randin CF, Vitasse Y, Zimmermann NE (2016) Where, why and how? Explaining the low-temperature range limits of temperate tree species. *Journal of Ecology* 104: 1076–1088. <https://doi.org/10.1111/1365-2745.12574>
- Leung B, Finnoff D, Shogren JF, Lodge D (2005) Managing invasive species: Rules of thumb for rapid assessment. *Ecological Economics* 55: 24–36. <https://doi.org/10.1016/j.ecolecon.2005.04.017>
- Liu C, Berry PM, Dawson TP, Pearson RG (2005) Selecting thresholds of occurrence in the prediction of species distributions. *Ecography* 28: 385–393. <https://doi.org/10.1111/j.0906-7590.2005.03957.x>
- Lloret F, Médail F, Brundu G, Hulme PE (2004) Local and regional abundance of alien plant species on Mediterranean islands: are species traits important? *Global Ecology and Biogeography* 13: 37–45. <https://doi.org/10.1111/j.1466-882X.2004.00064.x>
- Lombaert E, Guillemaud T, Thomas CE, Lawson Handley LJ, Li J, Wang S, Pang H, Goryacheva I, Zakharov IA, Jousset E (2011) Inferring the origin of populations introduced from a genetically structured native range by approximate Bayesian computation: case study of the invasive ladybird *Harmonia axyridis*. *Molecular Ecology* 20: 4654–4670. <https://doi.org/10.1111/j.1365-294X.2011.05322.x>
- Magory Cohen T, McKinney M, Kark S, Dor R (2019) Global invasion in progress: modeling the past, current and potential global distribution of the common myna. *Biological Invasions* 21: 1295–1309. <https://doi.org/10.1007/s10530-018-1900-3>
- Matthei J, Marticorena C, Quezada M, Rodríguez R (1995) Manual de las malezas que crecen en Chile. Alfabetra impresores.
- Merow C, Smith MJ, Silander JA (2013) A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography* 36: 1058–1069. <https://doi.org/10.1111/j.1600-0587.2013.07872.x>
- Norris D (2014) Model thresholds are more important than presence location type: Understanding the distribution of lowland tapir (*Tapirus terrestris*) in a continuous Atlantic forest of southeast Brazil. *Tropical Conservation Science* 7: 529–547. <https://doi.org/10.1177/194008291400700311>
- Önol B (2012) Effects of coastal topography on climate: high-resolution simulation with a regional climate model. *Climate Research* 52: 159–174. <https://doi.org/10.3354/cr01077>

- Ortega YK, Pearson DE (2005) Weak vs. strong invaders of natural plant communities: assessing invasibility and impact. *Ecological Applications* 15: 651–661. <https://doi.org/10.1890/04-0119>
- Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography* 12: 361–371. <https://doi.org/10.1046/j.1466-822X.2003.00042.x>
- Pertierra LR, Aragón P, Shaw JD, Bergstrom DM, Terauds A, Olalla-Tárraga MÁ (2017) Global thermal niche models of two European grasses show high invasion risks in Antarctica. *Global Change Biology* 23: 2863–2873. <https://doi.org/10.1111/gcb.13596>
- Peterson A, Soberón J, Pearson RG, Anderson R, Martinez-Meyer E, Nakamura M, Araújo MB (2011) *Ecological Niches and Geographic Distributions*. Princeton University Press, Oxford. <https://doi.org/10.23943/princeton/9780691136868.003.0003>
- Pearce J, Ferrier S (2000) Evaluating the predictive performance of habitat models developed using logistic regression. *Ecological Modelling* 133: 225–245. [https://doi.org/10.1016/S0304-3800\(00\)00322-7](https://doi.org/10.1016/S0304-3800(00)00322-7)
- Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190: 231–259. <https://doi.org/10.1016/j.ecolmodel.2005.03.026>
- Phillips SJ, Dudík M (2008) Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* 31: 161–175. <https://doi.org/10.1111/j.0906-7590.2008.5203.x>
- Pigott CD (1989) Factors Controlling the Distribution of *Tilia cordata* Mill at the Northern Limits of Its Geographical Range. IV. Estimated Ages of the Trees. *The New Phytologist* 112: 117–121. <https://doi.org/10.1111/j.1469-8137.1989.tb00316.x>
- Pyšek P, Jarošík V, Hulme PE, Pergl J, Hejda M, Schaffner U, Vilà M (2012) A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. *Global Change Biology* 18: 1725–1737. <https://doi.org/10.1111/j.1365-2486.2011.02636.x>
- Pyšek P, Richardson DM (2007) Traits associated with invasiveness in alien plants: where do we stand? In: Nentwig W (Ed) *Biological Invasions*. Springer Berlin Heidelberg, Berlin, Heidelberg, 97–125. https://doi.org/10.1007/978-3-540-36920-2_7
- Quintero I, Wiens JJ (2013) What determines the climatic niche width of species? The role of spatial and temporal climatic variation in three vertebrate clades: Climatic niche width of species. *Global Ecology and Biogeography* 22: 422–432. <https://doi.org/10.1111/geb.12001>
- Quiroz C, Pauchard A, Marticorena A, Cavieres LA (2009) *Manual de plantas invasoras del centro-sur de Chile*. Laboratorio de Invasiones Biológicas Concepción, Chile, 44 pp.
- Rasmussen KK, Kollmann J (2004) Poor sexual reproduction on the distribution limit of the rare tree *Sorbus torminalis*. *Acta Oecologica* 25: 211–218. <https://doi.org/10.1016/j.actao.2004.02.001>
- Rejmánek M, Richardson DM, Pyšek P (2005) Plant invasions and invasibility of plant communities. *Vegetation Ecology* 332355:
- Ricciardi A, Cohen J (2007) The invasiveness of an introduced species does not predict its impact. *Biological Invasions* 9: 309–315. <https://doi.org/10.1007/s10530-006-9034-4>

- Ricciardi A, Whoriskey FG, Rasmussen JB (1996) Impact of the (*Dreissena*) invasion on native unionid bivalves in the upper St. Lawrence River. *Canadian Journal of Fisheries and Aquatic Sciences* 53: 1434–1444. <https://doi.org/10.1139/f96-068>
- Richardson DM, Thuiller W (2007) Home away from home – objective mapping of high-risk source areas for plant introductions. *Diversity and Distributions* 13: 299–312. <https://doi.org/10.1111/j.1472-4642.2007.00337.x>
- Rigby RA, Stasinopoulos DM (2005) Generalized additive models for location, scale and shape. *Journal of the Royal Statistical Society: Series C (Applied Statistics)* 54: 507–554. <https://doi.org/10.1111/j.1467-9876.2005.00510.x>
- Schulze ED, Robichaux RH, Grace J, Rundel PW, Ehleringer JR (1987) Plant water balance. *BioScience* 37: 30–37. <https://doi.org/10.2307/1310175>
- Settele J, Hammen V, Hulme P, Karlson U, Klotz S, Kotarac M, Kunin W, Marion G, O'Connor M, Petanidou T (2005) ALARM: Assessing large-scale environmental Risks for biodiversity with tested Methods. *Gaia-Ecological Perspectives for Science and Society* 14: 69–72. <https://doi.org/10.14512/gaia.14.1.20>
- Slatyer RA, Hirst M, Sexton JP (2013) Niche breadth predicts geographical range size: a general ecological pattern. *Ecology Letters* 16: 1104–1114. <https://doi.org/10.1111/ele.12140>
- Soberón J (2007) Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters* 10: 1115–1123. <https://doi.org/10.1111/j.1461-0248.2007.01107.x>
- Stasinopoulos DM, Rigby RA (2007) Generalized additive models for location scale and shape (GAMLSS) in R. *Journal of Statistical Software* 23: 1–46. <https://doi.org/10.18637/jss.v023.i07>
- Thuiller W, Gassó N, Pino J, Vilà M (2012) Ecological niche and species traits: key drivers of regional plant invader assemblages. *Biological Invasions* 14: 1963–1980. <https://doi.org/10.1007/s10530-012-0206-0>
- Thuiller W, Lavorel S, Araujo MB (2005) Niche properties and geographical extent as predictors of species sensitivity to climate change. *Global Ecology and Biogeography* 14: 347–357. <https://doi.org/10.1111/j.1466-822X.2005.00162.x>
- Tingley R, Vallinoto M, Sequeira F, Kearney MR (2014) Realized niche shift during a global biological invasion. *Proceedings of the National Academy of Sciences* 111: 10233–10238. <https://doi.org/10.1073/pnas.1405766111>
- Turnbull LA, Crawley MJ, Rees M (2000) Are plant populations seed-limited? A review of seed sowing experiments. *Oikos* 88: 225–238. <https://doi.org/10.1034/j.1600-0706.2000.880201.x>
- Valdovinos FS, Berlow EL, Moisset de Espanés P, Ramos-Jiliberto R, Vázquez DP, Martinez ND (2018) Species traits and network structure predict the success and impacts of pollinator invasions. *Nature Communications* 9: 2153. <https://doi.org/10.1038/s41467-018-04593-y>
- van Kleunen M, Weber E, Fischer M (2010) A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters* 13: 235–245. <https://doi.org/10.1111/j.1461-0248.2009.01418.x>
- Vazquez DP (2006) Exploring the relationship between niche breadth and invasion success. *Conceptual ecology and invasion biology: reciprocal approaches to nature*. Springer, 307–322. https://doi.org/10.1007/1-4020-4925-0_14

- Vela Díaz DM, Blundo C, Cayola L, Fuentes AF, Malizia LR, Myers JA (2020) Untangling the importance of niche breadth and niche position as drivers of tree species abundance and occupancy across biogeographic regions. *Global Ecology and Biogeography* 29: 1542–1553. <https://doi.org/10.1111/geb.13139>
- Wiens JJ, Ackerly DD, Allen AP, Anacker BL, Buckley LB, Cornell HV, Damschen EI, Jonathan Davies T, Grytnes J-A, Harrison SP, Hawkins BA, Holt RD, McCain CM, Stephens PR (2010) Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters* 13: 1310–1324. <https://doi.org/10.1111/j.1461-0248.2010.01515.x>
- Williamson MH, Fitter A (1996) The characters of successful invaders. *Biological Conservation* 78: 163–170. [https://doi.org/10.1016/0006-3207\(96\)00025-0](https://doi.org/10.1016/0006-3207(96)00025-0)

Supplementary material 1

Table S1. Exotic species located in Quadrant 1 (see Figure 3) and impacts on biodiversity, agriculture and cattle raising

Authors: Ramiro O. Bustamante, Lúa Alves, Estefany Goncalves, Milen Duarte, Ileana Herrera

Data type: occurrence

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Link: <https://doi.org/10.3897/neobiota.63.50049.suppl1>

Supplementary material 2

Table S2. Basic information obtained for 49 exotic plants in Chile

Authors: Ramiro O. Bustamante, Lúa Alves, Estefany Goncalves, Milen Duarte, Ileana Herrera

Data type: species data

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Supplementary material 3

Map of the species

Authors: Ramiro O. Bustamante, Lúa Alves, Estefany Goncalves, Milen Duarte, Ileana Herrera

Data type: occurrence

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